

New information about *Echinochiton dufoei*, the Ordovician spiny chiton*

John Pojeta, Jr.¹ and Jimmie DuFoe²

¹ U.S. Geological Survey and Department of Paleobiology, Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A., pojetaj@si.edu

² 417 Grove Street, Rockton, Illinois 61072, U.S.A., jdufoe2001@yahoo.com

Abstract: *Echinochiton dufoei* Pojeta *et al.*, 2003 is now known from seven specimens. The new material shows the anterior end and allows for a full reconstruction of the animal. The hollow spines are circumsomal; they were flexible and perhaps moveable in rotary anterior-posterior directions. Possible functions for the hollow spines are discussed. The relationships of *E. dufoei* to other chitons and to other molluscs and mollusc-like organisms are presented.

Key words: Mollusca, Polyplacophora, Fossil, Wisconsin

Echinochiton dufoei Pojeta *et al.*, 2003 was based on four partial specimens, three of which are parts and counterparts. None of these preserved the anterior hollow spines or fully preserved the anterior valves, and none indicated that the spines were flexible. Three new specimens are now known. Two consist of parts and counterparts (USNM 533989 and 533990; Figs. 1-2); they preserve the anterior valves and spines (Pojeta and DuFoe 2006) and show that the hollow spines were flexible. The third specimen (USNM 533991) is fragmentary; it preserves three valves in oblique cross section and partial impressions of a pair of spines and is not figured. Herein, the 2003 reconstruction of *E. dufoei* is shown, as is the new reconstruction.

Repositories: The specimens figured herein are repositied at the Department of Paleobiology, United States National Museum of Natural History (USNM), Washington, D.C. or at the Burpee Museum of Natural History (BMNH), Rockford, Illinois, U.S.A.

MATERIALS AND METHODS

All seven known “crack-out” specimens of *Echinochiton dufoei* were collected from a 7-15 cm thick mollusc-rich bed of dolostone near the top of Bauer’s Quarry west of Beloit, Wisconsin, in the Forreton Member of the Grand Detour Formation, Platteville Group, of Middle Ordovician (Turinian; Blackriveran) age (Hoare and Pojeta 2006). Catalani and Frey (1998) noted that the Forreton Member was deposited in a tropical, shallow-water, carbonate platform environment. Kolata (1975: 11) wrote that studies of the Platteville Group and the lower part of the overlying Galena Group

“strongly suggest an open platform, shallow to deep subtidal, normal marine environment. . .”

Most fossils in the 7-15 cm bed are found parallel to bedding and occur in “pockets of accumulation.” Cephalopods and pelecypods are the most abundant and diverse molluscs in the bed; 44% of the 25 known genera of cephalopods in the Forreton Member occur in this thin bed (DuFoe *et al.* 2006). Pelecypods are well represented by several species of palaeotaxodonts and pteriomorphians. Gastropods and bellerophonts are less abundant. Rostroconchs are known from a few specimens of *Eopteria* Billings, 1865. To date, chitons are the only group that has been studied in detail (Pojeta *et al.* 2003, Hoare and Pojeta 2006); this class is represented by three species, none of which is abundant. All of the molluscs are preserved as molds and casts.

The non-molluscan fauna includes strophomenoid brachiopods, bumastid trilobites, ostracodes, and fragmentary bryozoans and corals usually having well-preserved exoskeletons.

INTERPRETATION OF THE SHELL BED

The 7-15 cm shell bed is a death assemblage or *thana-tocoenosis*. The fossils occur in “pockets of accumulation” separated by areas with few or no shells. The pockets indicate an irregular sea bottom with the shells accumulating in the low areas.

That the shells have been moved to their present location is likely because most valves of the pelecypods are disarticulated, as are the valves of the few brachiopods. Except *Echinochiton dufoei*, the chiton remains are disarticulated

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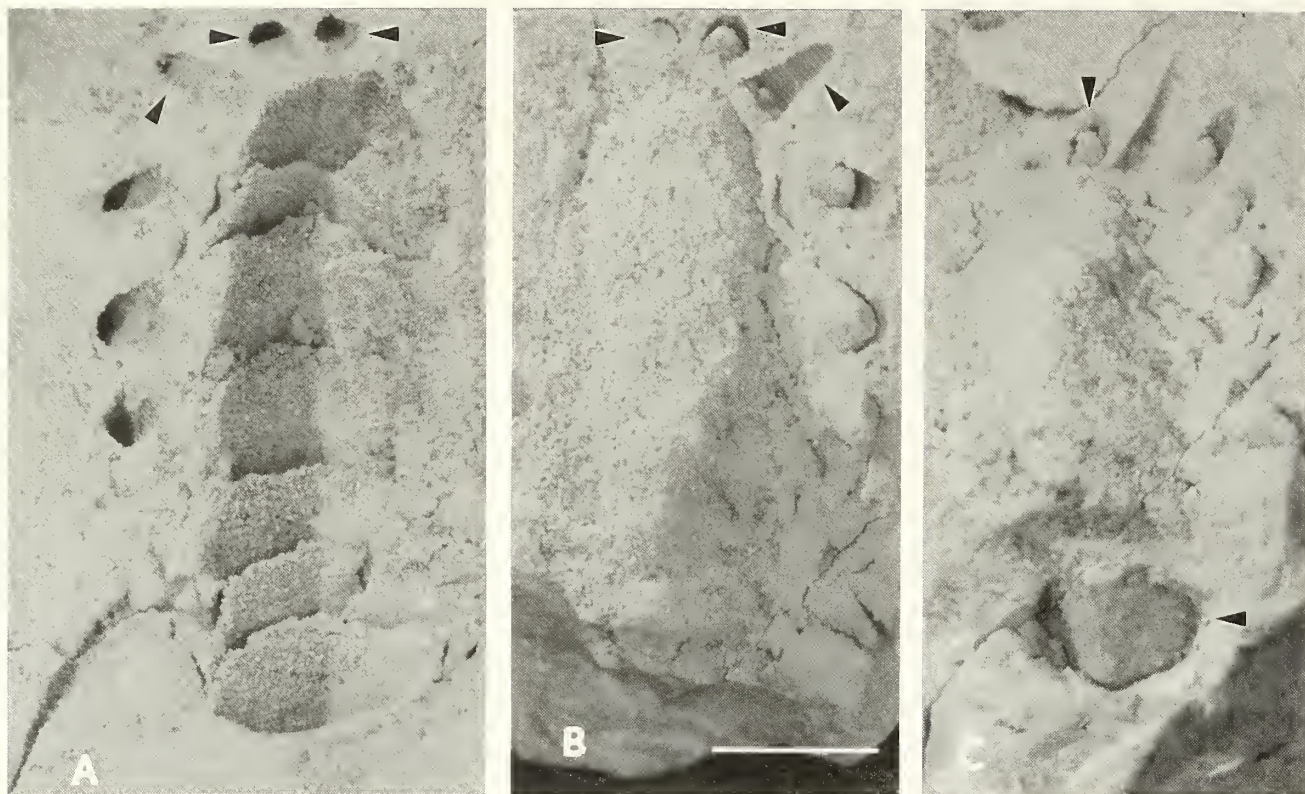


Figure 1. *Echinochiton dufoei* topotype (USNM 533989), anterior end up; scale bar 5 mm applies to all three views. A, Part, showing the anteriorly rounded head valve and valves 2-7 as internal molds of their ventral sides. Oblique arrow points to external mold of the morphologically right-lateral head valve spine. Horizontal arrows point to holes left by anterior head valve spines; these spine impressions are vertical to bedding. B, Counterpart filling of the body space below the valves. Arrows point to the same features seen in A; anterior spine impressions are filled with sediment. C, Counterpart tilted away from observer in order to show the tail valve (horizontal arrow), which is preserved at right angles to bedding. Vertical arrow marks the right-lateral sediment-filled anterior spine of the head valve.

plates. Most of the cephalopods are preserved as short fragments of phragmocone attached to short sections of the living chamber. The gastropods have abraded apertures. The trilobites are usually disarticulated into their constituent parts, and the corals and bryozoans are fragmented. That the assemblage was not moved far is indicated by some of the pelecypods that remained articulated or are preserved with the two valves splayed open and lying side by side (butterflyed) parallel to bedding and with the umbos touching.

Echinochiton dufoei is an exception to the general preservation of the other fauna, in that all known specimens are partially articulated although disarticulated spines are known.

THE NEW SPECIMENS

As in previous specimens, the new material is preserved as complex molds. In specimen USNM 533989 (Figs. 1A-C) the counterpart (Figs. 1B-C) shows impressions, or sedimen-

tary fillings, of five of the hollow spines on the right side, including a right-lateral spine on the head valve, and two spines at the anterior end of the head valve. The sedimentary filling of the body space does not show the valves well. The part of the specimen (Fig. 1A) shows the undersides of the anteriorly rounded head valve and valves 2-7 parallel to bedding. The tail valve is at right angles to bedding and is preserved on the counterpart (Figs. 1B-C). The external mold of the right-lateral spine on the head valve is preserved as an impression. Anterior to the head valve are the impressions and fillings of two spines (Figs. 1A-B).

The length of the eight valves is about 25 mm, the width of a single intermediate valve is 6 mm, and the length of the one complete and curved spine preserved parallel to bedding on the right side of valve 6 (Fig. 1A) of the part is 7.5 mm.

It is noteworthy that the impressions of the spines, or their sedimentary fillings, of this specimen are preserved at various angles to bedding, ranging from parallel to right angles (Figs. 1A-B), thus indicating that the spines were

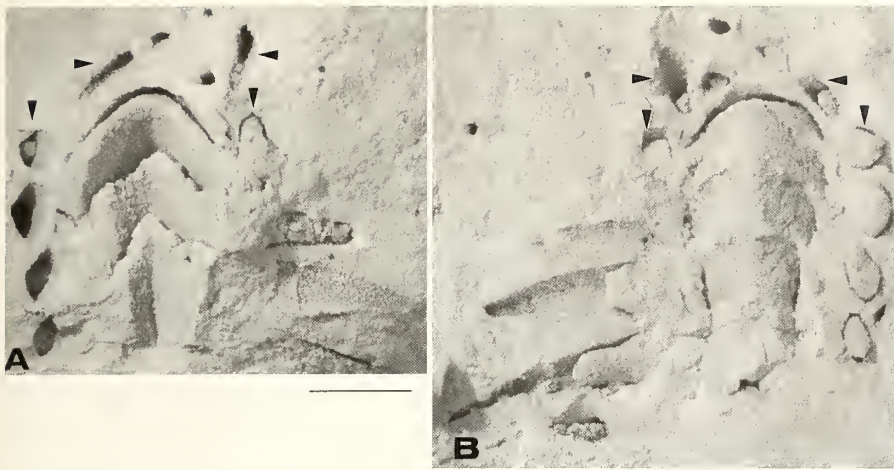


Figure 2. *Echinochiton dufoei* topotype (USNM 533990), anterior end up; scale bar 5 mm applies to both views. A, Part, showing the anteriorly rounded head valve and valves 2 and 3 as internal molds of their ventral sides. The lateral head valve spines (vertical arrows) are preserved vertical to bedding as are the spines on the morphologically right side. The spines on the morphologically left side of valves 2 and 3 are preserved parallel to bedding. The anterior head valve spines are preserved rotated counterclockwise to the morphologically left side and have most of their lengths are exposed (horizontal arrows). B, Counterpart filling of the body space below the valves showing the anteriorly rounded head valve. Arrows mark the same features as in A above. Left-lateral external molds of spines partially filled with sediment.

flexible. All previously known specimens of *Echinochiton dufoei* have the hollow spines preserved parallel to bedding (Pojeta *et al.* 2003, figs. 1-6). As used herein, the word flexible means that at least after death the spines were capable of being bent. Specimen USNM 533990 (Figs. 2A-B), part and counterpart, preserves the anteriorly rounded head valve, valves 2-3 on the part (Fig. 2A), and the head valve and valves 2-4 on the counterpart (Fig. 2B). On the left side of the counterpart, the hollow spines attached to valves 2-4 are preserved parallel to bedding and show some of the sediment fillings of the bases of the spines. On the right side, the sediment fillings of the spines of valves 2-4 are preserved at right angles to bedding (Fig. 2B). The lateral spines of the head valve are preserved at right angles to bedding. The anterior spines of the head valve have been rotated counterclockwise to the left (Fig. 2B); they are at a low angle to bedding and much of their lengths are exposed. This specimen also shows that the spines were flexible, because they are preserved at various angles to bedding.

The length of the four preserved valves is 14 mm (valve 4 is incomplete), the width of valve 2 is 6 mm, and the length of the spine on the left side of valve 4 (Fig. 2B) is about 11 mm (attachment to valve 4 not visible).

Neither of the new specimens described here show well-preserved scutes or the slots made by scutes in internal molds; a few slots are on the right side (left side in view, Fig.

1A). The scutes are erect structures that occur in right and left rows between and parallel to the valves and between the valves and the hollow spines (Figs. 3A, 3B). The sediment-filled hollow spines are best preserved on the holotype part (BMNH 1996.045.01) and counterpart (BMNH 1996.045.02) and are parallel to bedding (Figs. 3A, 4).

See Figure 5 for the new reconstruction and the 2003 reconstruction.

MOVEABLE SPINES?

So far as is known, *Echinochiton dufoei* is unique among chitons in its possession of circumsomal hollow spines that are as long, or longer, than the valves are wide (Figs. 1-5). Our search of the literature yielded no other chitons with the large, hollow spines of *E. dufoei*. Eernisse (e-mail comm., September 2006), commenting on *E. dufoei*, noted: "There are no

other hollow spines documented [in chitons] that I know of. We (with Pat Reynolds) cite studies in my chapter on chitons: Eernisse, D. J., and P. D. Reynolds, 1994."

Scheltema *et al.* (1994: 20) noted the existence of solid and hollow spicules in the epidermis of neomenioid aplacophorans. However, these are small structures, about 20-200 microns long "and are secreted extracellularly within an invagination of a single cell." Thus, it is highly unlikely that the hollow spicules of aplacophorans are homologous with the hollow spines of *Echinochiton dufoei*.

The new specimens show that the spines were flexible. However, were they moveable in life, or is the flexibility a post-mortem effect? Examine the color photographs of the holotype part and counterpart before the specimen was prepared and before it was whitened with ammonium chloride sublimate (Fig. 6); compare this with the prepared specimen (Figs. 3A and 4). It is noteworthy that the impressions of the spines are much darker than the surrounding rock and the valves; this is also the case with some of the spines (Fig. 2) and the specimens in Pojeta *et al.* (2003: figs. 5.2, 6.3, 6.4).

This darker color suggests that the spines contained more organic matter than did the valves. In some Ordovician mytiliform and modioliform pelecypods, the internal molds and the ligament area are covered with a black film (Pojeta 1962: 175; Pojeta 1971: pl. 15, figs. 5, 6). This

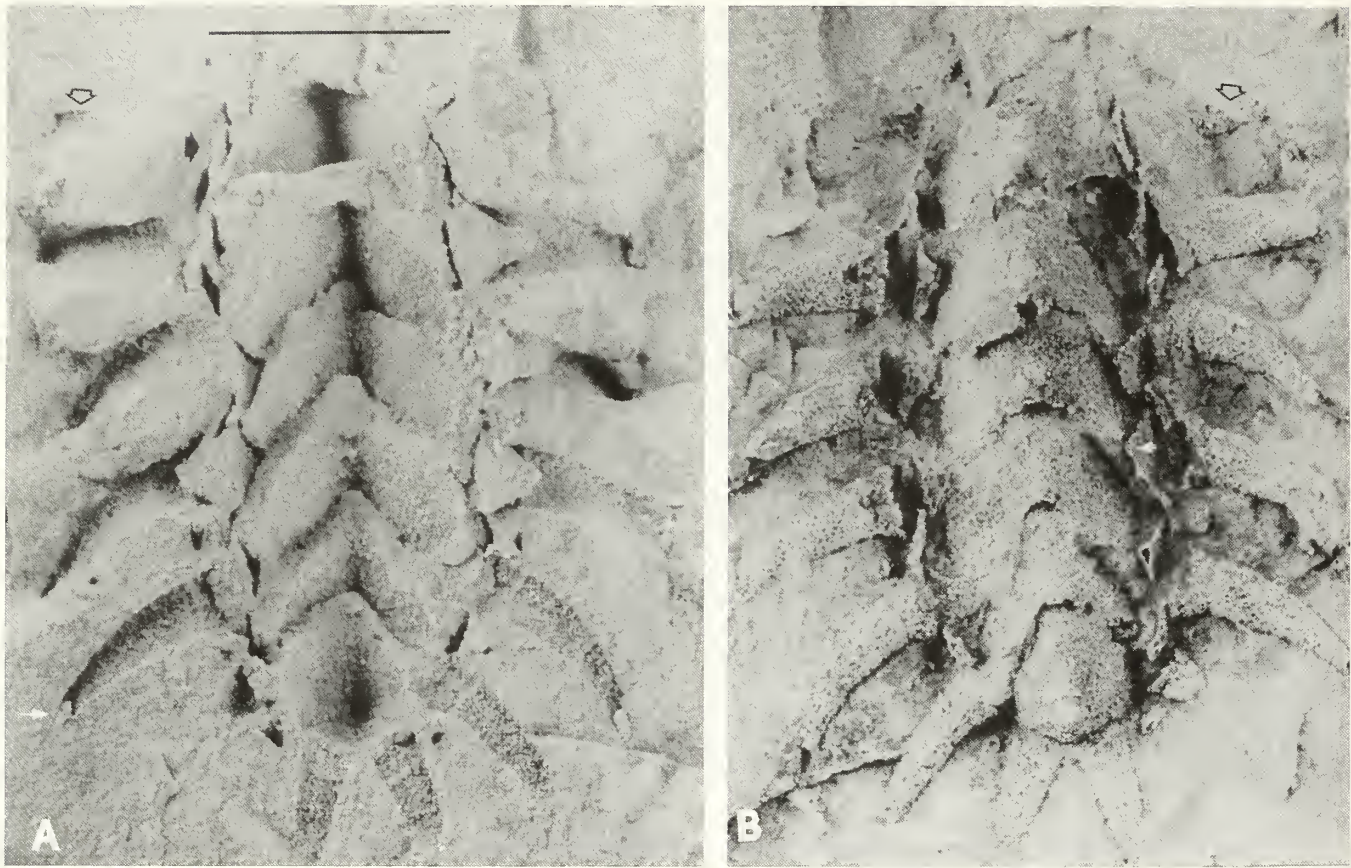


Figure 3. *Echinochiton dufoei* holotype (BMNH 1996.045.01), anterior end up; scale bar 10 mm applies to both views. A, Part, showing valves 3-8 as internal molds of their ventral sides, mucro of tail valve, external mold impressions of spines parallel to bedding, posterior spines of tail valve, partial sediment fillings of hollow spines, and slots paralleling the right and left lateral side of the valves (solid black arrow). Open black arrow points to a remnant impression of the morphologically right side spine of valve 3. White arrow at the tip of the external mold of the morphologically right side spine of valve 7 shows that the sediment filling of the spines went to their distal ends; thus, the spines were hollow to their tips. B, Latex cast of A, white arrow points to one of the scutes on the right side. Open black arrow at top right marks the same structure as in A.

presumed organic film does not extend into the surrounding sediment; it is limited to the internal mold. The ligament and the thick periostracum of extant mytiliform and modioliform pelecypods contains more organic material than in other areas of the shell and in other groups of pelecypods. This possible larger organic component of the spines in *Echinochiton dufoei* may help explain the flexibility of the spines.

The part of the holotype (Fig. 3A) preserves external impressions of the hollow spines, the underside of the valves, and rows of slots between the valves and the spines. The latex positive (Fig. 3B) shows that the slots are molds of right and left rows of raised triangular scutes between the valves and the spines. The scutes can occur between the spines or between the spines and the valves.

The spines show growth lines; thus, it seems likely that

mantle extended into them at least to the bases of the spines (Fig. 7A). If this tissue had sufficient muscle fibers, it could have moved the spines with the scute acting as a fulcrum against which to raise and lower them cantilever style or to move the spines fore and aft in a rotary fashion. The scutes bend toward the valves and together with the spine could form a ball-and-socket joint, analogous to what is seen in regular echinoids in which the solid spine is mounted on a tubercle (Hyman 1955, fig. 187A). In echinoids, the outer cylinder of muscle fibers, by local contraction, causes the spine to point in the direction of the stimulus (Hyman 1955: 438).

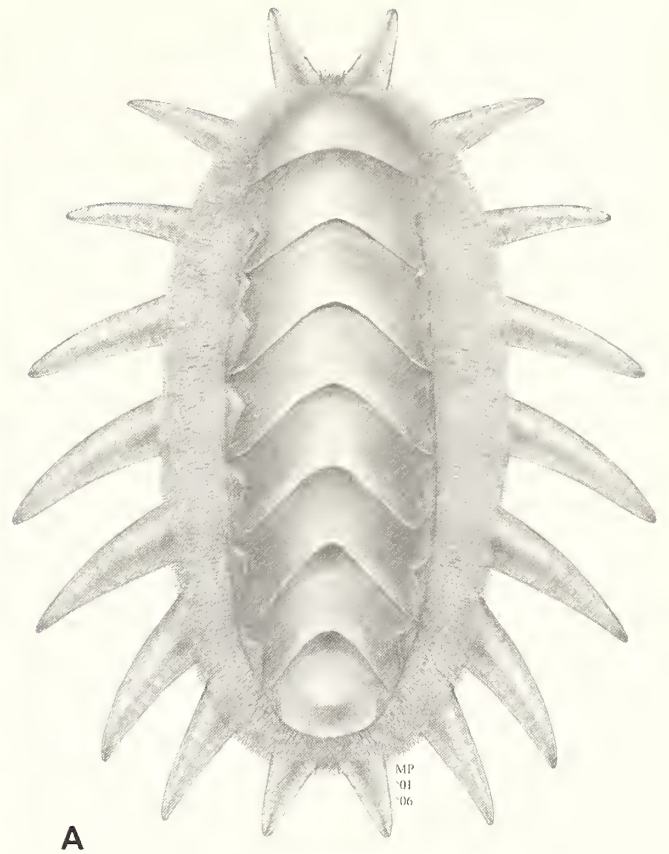
In both our old and new reconstructions (Fig. 5), we show the spines as being embedded in the mantle girdle. It is unlikely that they would be below the girdle, because this would impede the ability of the animal to attach to the



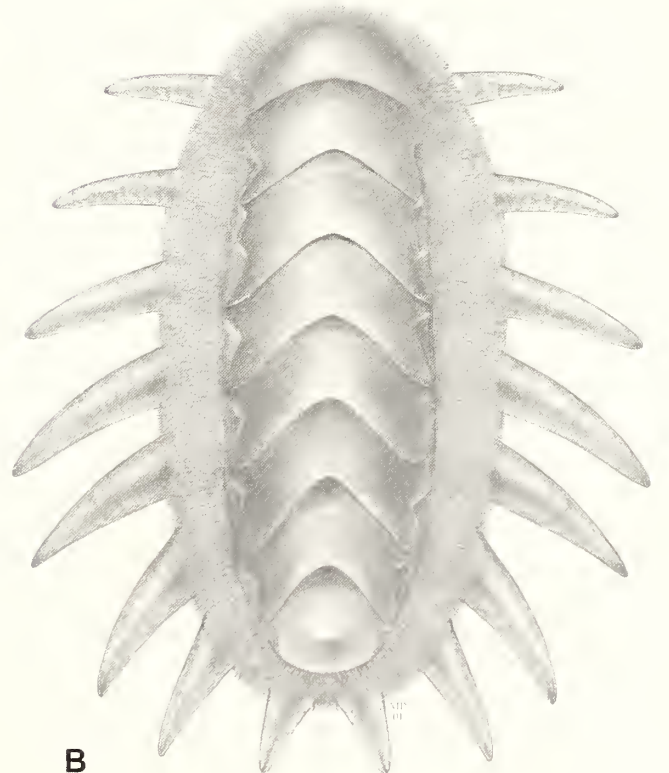
Figure 4. *Echinochiton dufoei* holotype (BMNH 1996.045.02), anterior end up; scale bar 10 mm. Counterpart filling of the body space below the valves of Fig. 3A. White arrow on the left lateral spine of valve 7 shows that the lumen of the spine decreased in size distally because the sediment filling decreases in size.

substrate. If the spines were embedded in the girdle, vertical movements would probably be limited and movement would be mostly in rotary anterior and posterior directions. Thus, the spines preserved at right angles to bedding would be largely a post-mortem effect. It is unlikely the spines were

Figure 5. *Echinochiton dufoei*. A, New reconstruction incorporating the new information from specimens seen in Figs. 1 and 2. Anterior end up. B, 2003 (Pojeta *et al.*) reconstruction showing the lack of information about the anterior end of the species. The lateral spines on the head valve were postulated, but not seen, in 2003. Size about 2.0×.



A



B



above the girdle, because there seems to be no way that they could have attached to the shell in this position and have mantle extend into them. The presence of spicules and scales in the girdle is indicated by small horizontal markings at nearly right angles to the lateral edges of the valves (Pojeta *et al.* 2003: figs. 6.1 and 7.2; Figs. 7B, 8 herein).

WHY LARGE HOLLOW SPINES?

What function could the large hollow spines serve? Various reasons can be postulated although none of the hypotheses stand out as the most likely reason for such spines:

(1) Somehow the spines were used for protection from predation. However, all known specimens of *Echinochiton dufoei* are small, in the 25–40 mm range. The major predators in Ordovician time were shelled cephalopods, many of which were considerably larger than *E. dufoei*. The cephalopods found in the same bed as *E. dufoei* range in size from a few centimeters to over three meters, and *E. dufoei* would not even be a small snack for most of the cephalopods except young juveniles. In addition, hollow spines, even if made turgid with fluid, would provide little protection from predation. Thus, it seems unlikely that the spines were used for protection. Also, as suggested above, because the spines were probably embedded in the girdle, their vertical movement would be limited and most movement would be in oar-like anterior and posterior directions.

K. M. Brown (Louisiana State University) suggested that “the horizontal spines would make it harder to pry the animal from the substrate” (pers. comm., June 2007)

Various non-chiton molluscs have spines, including spondylid and some venerid pelecypods, some muricid gastropods, and a few shelled cephalopods. These spines may or may not have a lumen, or a longitudinal groove. All are strongly calcareous and range in shape from sharply pointed to spatulate. Generally these are regarded as protective or supportive in function.

The spines of productoid brachiopods are hollow, hard, and not flexible when fully formed. Muir-Wood and Cooper (1960: 16) regarded the spines as: “Forming a prominent part of the ornament and occur to some extent in every productoid species. The spines were in part protective, but

Figure 6. *Echinochiton dufoei*, anterior end up; scale bar 10 mm applies to both images. A, B, Color photographs of part and counterpart of holotype (BMNH 1996.045) as the specimen was found in the field and before it was prepared. Compare to Fig. 3A and 4. Note that many of the spine impressions are much darker than the impressions of the valves and the surrounding sediment.



Figure 7. *Echinochiton dufoei* paratype (USNM 517481). A, Anterior to right; scale bar 10 mm. Enlargement of three lateral spine external molds showing growth lines. B, Anterior down; scale bar 10 mm. Underside of first three valves seen on the right side of Fig. 8, showing growth rugae. Lateral to the upper two valves, on the left side of the image, are marginal markings interpreted to be the impressions of scales and spicules. Black tailless arrow marks the same position as the black tailless arrow in Fig. 8.

they also played an important role in the attachment and support of the shell, and some may have functioned as strainers.” Grant (1966) showed the support function of the multitudinous spines of the productoid *Waagenoconcha abichi* in soft sediments.

(2) David Pawson, USNM (pers. comm., September 2006) has observed that, among other functions, some regular echinoids use their spines to define their living space and form a checkerboard-like pattern on the sea floor. This seems unlikely for *Echinochiton dufoei* because it is such a rare element in the fauna of the 7–15 cm thick bed; in 15 years of collecting and breaking literally tons of rock from the 7–15 cm thick bed, only seven specimens have been found. Of course, *E. dufoei* may be found to be abundant elsewhere. However, the Ordovician fossils of Wisconsin and Illinois have been studied for at least 140 years, and the first mention of *Echinochiton* in the literature is Pojeta *et al.* (2003).

(3) The function of the spines is as stabilizers—something akin to outriggers when the animal moved. Alternatively, the spines may have helped to maintain the chiton’s position on a hard substrate in strong waves and currents. However, extant chitons hug the substrate tenaciously using the foot and mantle girdle and are difficult to dislodge without using an instrument having a blade.

(4) The spines were somehow used as accessory organs of locomotion, particularly if their motion was largely in the rotary anterior-posterior directions.

TAXONOMIC PLACEMENT

Echinochiton dufoei is a polyplacophoran mollusc be-

cause of the row of eight bilaterally symmetrical valves (plates), the mucro on the tail valve, and the likely presence of a mantle girdle interpreted from small impressions lateral to the valves indicating the presence of spicules and scales. It differs from other polyplacophorans in the presence of circumosomal, large, hollow spines, and the right and left rows of scutes paralleling the outer edges of the valves. Thus, it is placed in the separate family Echinochitonidae.

Within the Polyplacophora, *Echinochiton dufoei* is in the subclass Paleoloricata based on the upright valves with large apical areas (Fig. 8); none of the known specimens show sutural laminae and they lack insertion plates. It is treated as a member of the order Chelodida because the intermediate

valves are not clearly differentiated into lateral and central areas (Figs. 1A, 2B)

When commenting on *Echinochiton dufoei*, Sirenko (2006: 33) misunderstood Pojeta *et al.* (2003). His thought that the specimens were external molds is only partially correct. The specimens are very complex molds; the only part of the molds that are clearly external are the impressions of the outside of the spines when parallel to bedding (Fig. 3A). The sedimentary fillings of the spines are internal molds (Fig. 4). The specimens are internal molds of the ventral sides of the valves (Figs. 1–4).

To date, most of the external molds of the dorsal side of the valves have been found in a specimen where they cannot be seen (Fig. 8). An exception to this is the partial impression of the external surface of the head valve (Fig. 1A); it does not preserve the external features.

Sirenko’s notation that *Echinochiton dufoei* has small apical areas is incorrect as shown herein by the specimen (Fig. 8) in which the valves are seen in lateral view. The valves are nearly erect and have large apical areas. The spaces between the internal and external molds represent a minimum thickness for the valves. In this specimen, the external molds of the valves could not be exposed.

The valves that are preserved parallel to bedding so that they cannot be seen in lateral view may have been distorted by compaction (compare the shapes of the valves in Figs. 1A, 2A, and 3A). Also when comparing the shapes of the counterparts (Figs. 2B, 3B, 4), there is variation in the shapes of the valves.

In *Echinochiton dufoei*, Sirenko suggested the presence of incisura; it is not clear to us what the term incisura means.



Figure 8. *Echinochiton dufoei* paratype (USNM 517481), anterior end to right; scale bar 10 mm. Lateral view of four valves showing their nearly erect posture and the filling of the body space below the valves. Downward facing straight-tailed barbed arrow points to two sediment fillings of the valve suggesting the presence of two openings into the valve as in *Matthevia variabilis* Walcott, 1885. Downward facing straight-tailed unbarbed arrow points to markings lateral to the body that are interpreted as having been made by spicules in the girdle. Wavy arrow at left end points to a piece of a fifth valve that is only partially preserved. Solid triangular tailless arrow is at the same position as in Fig. 7B.

Hyman (1967: 74) used the term incisures as follows: "The insertion plates are commonly cut into teeth by incisures . . . These incisures are continued . . . as slit grooves known as slit rays." *Echinochiton dufoei* does not show insertion plates and, thus, lacks slit rays separating the insertion teeth from the rest of the shell (Fig. 1A).

PHYLOGENETIC RELATIONSHIPS

Echinochiton shows similarities to mattheviids which are the oldest known chitons. In *Matthevia* Walcott, 1885, the valves are nearly upright and they have large apical areas (Runnegar *et al.* 1979, Vendrasco *et al.* 2004) as does *Echinochiton* (Fig. 8). The suggestion of a relationship between *Echinochiton dufoei* and *Matthevia* is reinforced by a plate of *E. dufoei* which shows the filling of two holes in the valve (Fig. 8) as is the case in *Matthevia variabilis* Walcott, 1885, the type species of *Matthevia*. Hoare (2000) placed mattheviids at the base of his phylogenetic scheme of polyplacophorans.

Caron *et al.* (2006) discussed and redefined the large, Middle Cambrian, Burgess Shale species *Odontogriphus omalus* Conway Morris, 1976. This animal approximates a shell-less polyplacophoran. Caron *et al.* (2006) noted that the species is up to 125 mm long, is flattened dorso-ventrally, and has a dorsal stiffened cuticle, a radula, a straight gut, and simple gills that are present in a groove running laterally and posteriorly around a muscular foot. Stratigraphically, *Odontogriphus* Conway Morris is older than the first known chitons which occur in Upper Cambrian rocks (Vendrasco and Runnegar 2004). At the very least, an animal closely resembling *Odontogriphus* would be a likely stem group for chitons.

Echinochiton increases the known disparity of polyplacophorans. Vendrasco *et al.* (2004) considered Paleozoic chiton disparity to be even greater than that suggested by *Echinochiton*, after the discovery of a nearly complete Early Mississippian specimen of the taxon *Multiplicaphora* Hoare and Mapes, 1995.

The new species *Polysacos vickersianum* Vendrasco *et al.*, 2004, is about 25 mm long. The shell has three longitudinal columns of valves plus head and tail valves, and it is surrounded by many elongate hollow spines. The authors noted the similarity of this arrangement to *Echinochiton dufoei* in which the skeleton has a central column of valves, two flanking columns of small dorsally projecting scutes, and is surrounded by hollow spines that grew by accretion. In both groups the anterior and posterior valves are morphologically distinct from the intermediate valves. Vendrasco *et al.* (2004) regarded the skeleton of *E. dufoei* as intermediate in form between the skeletons of multiplacophorans and typical chi-

tons. As in “crown group chitons”, multiplacophorans have pores in valve surfaces and possess the articulamentum (inner shell layer) that projects from the growing margin of the shell. *Echinochiton* and other stem group chitons are not known to have the articulamentum.

As noted by Vendrasco *et al.* (2004), there are significant differences between chitons and multiplacophorans such as *Polysacos*. The most striking difference is that in *Polysacos* there is a seven-fold, rather than an eight-fold iteration of the major skeletal elements.

The cladistic analysis performed by Vendrasco *et al.* (2004: 288) “Strongly supports the placement of multiplacophorans with the total group Polyplacophora.” They treat the Multiplacophora as an order within the class Polyplacophora.

Another recently-discovered Paleozoic multi-plated species is *Acaenoplax hayae* Sutton *et al.*, 2001. Sutton *et al.* (2004) monographed the species. The species is known from Middle Silurian age rocks. This species is vermiform, up to 40 mm long, and has one ventral and seven dorsal valves. The dorsal valves are not articulated and most are separated by a variable number of dorsal ridges. Most of the ridges bear elongate, thin, rigid, and pointed spines, and although it is not noted if the spines were hollow, this seems unlikely. Sutton *et al.* (2001a) regarded *Acaenoplax* Sutton *et al.*, 2001 as a mollusc, perhaps allied to the Aplacophora and showing some polyplacophoran affinities.

Subsequent to Sutton *et al.* (2001a), there was a debate about the treatment of *Acaenoplax* as a mollusc. Steiner and Salvini-Plawen (2001) argued that *Acaenoplax hayae* was best considered to be allied to polychaete annelids; Sutton *et al.* (2001b, 2004) defended the molluscan affinities.

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